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## *Dupuya*, a New Genus of Malagasy Legumes (Fabaceae)

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**ABSTRACT.** The new endemic Malagasy genus *Dupuya* is proposed based on morphological characters. It has two species, *D. haraka*, comb. nov., and *D. madagascariensis*, comb. nov., and is distinguished from related genera in having no petals, numerous stamens, a whorl of staminodes inside the stamens, and a number of distinctive seed characters. A new combination is also made for *Dupuya madagascariensis* subsp. *tamarindoides*. *Dupuya* is a member of the aldinoid clade with the genera *Aldina*, *Amburana*, *Cordyla*, *Dussia*, *Mildbraediodendron*, and *Myrospermum*.

**Key words:** aldinoid clade, *Cordyla*, *Dupuya*, *Dupuya haraka*, *Dupuya madagascariensis*, Fabaceae, Leguminosae, Madagascar.

In 2002, the outstanding *Leguminosae of Madagascar* was published (Du Puy et al., 2002). This comprehensive treatment fills a critical lacuna in our knowledge of the world's legumes; 34% of the 100 native Malagasy genera and 80% of the 573 native species are endemic. All taxa were described in detail, and the fruit and seed descriptions are some of the most complete descriptions found in any floristic work. I compared all their descriptions to those in our database of legume genera (Kirkbride et al., 2003). For all the Malagasy genera, only minor revisions were needed to encompass the variations found in Madagascar, with one notable exception, *Cordyla* Loureiro, for which our seed data were completely at odds with Du Puy and Labat's (2002) descriptions and illustrations of the genus and its two constituent species in Madagascar. Du Puy and Labat (2002: 294) had noted, "the Malagasy species are distinctive as the inner stamens are sterile." Examination of the USDA, ARS, U.S. National Seed Herbarium (BARC) material revealed that our seed data were based only on African specimens of *Cordyla*, and corresponded with that of Corner (1976) for *C. africana* Loureiro. After examining specimens of all five African *Cordyla* species (see Appendix 1), as well as the two in Madagascar, it was apparent that Du Puy and Labat (2002) had correctly described the latter and that our data for the African members were also correct. Based on the presence of staminodes in the Mala-

gasy species and their absence in the African species, along with the many differences in the seeds of the two groups (see the key to genera below), the two Malagasy species are here described as *Dupuya* J. H. Kirkbride, a new genus endemic to Madagascar.

### SYSTEMATIC HISTORY OF *CORDYLA* S.L.

Loureiro (1790) described the genus *Cordyla* with a single species, *C. africana*. Milne-Redhead (1937) speculated that Loureiro collected the type specimen in Mozambique because the common name that he used for it, "mutonda," was still in use for it there. Milne-Redhead (1937) revised the four African species known to him, and later Gillett (1960) added a fifth, *C. somalensis* J. B. Gillett. Viguier (1948) described the first Malagasy species, *C. madagascariensis* R. Viguier, and Capuron (1968) published the second, *C. haraka* Capuron, in his revision of Malagasy *Cordyla*. Following Capuron, all other *Cordyla* treatments have been floristic in nature (Aubréville, 1970; Berhaut, 1975; Brenan, 1967; Brunel et al., 1984; Cowan, 1981; Du Puy & Labat, 2002; Gilbert & Boutique, 1952; Gillett, 1960, 1962; Hedburg & Edwards, 1989; Hutchinson, 1964; Keay, 1958, 1989; Keay et al., 1964; Lebrun & Stork, 1992; Ross, 1977; Thulin, 1993) without attempting to compare or re-evaluate its generic delimitation based on an analysis of all its members.

Herendeen (1995) carried out extensive phylogenetic analyses of the 11 genera in tribe Swartzieae sensu Cowan (1981). He used 29 morphological characters, including 3 from seeds and 1 from the fruit. In addition, 19 Sophoreae and 3 Caesalpinieae genera were scored. The Sophoreae genera were included because Herendeen (1995: 123) considered them to be "the likely sister group to Swartzieae" and some genera, such as *Ateleia* (DC.) Bentham, *Cyathostegia* (Bentham) Schery, and *Holocalyx* Micheli, were difficult to place in the correct tribe. The Caesalpinieae genera served as outgroups. The Swartzieae genera fell into three distinct clades in association with various genera of Sophoreae and *Orphanodendron* Barneby & J. W.

Grimes. Swartzieae is obviously a polyphyletic group, and Herendeen (1995: 130) proposed that "the concept of Swartzieae . . . should be abandoned and all members of Swartzieae should be referred to Sophoreae."

In Herendeen's analyses, *Cordyla* formed a clade with *Mildbraediodendron* Harms, well supported by three nonhomoplasious forward changes: absence of a corolla, stamens united basally, and fruit globose to elongate with a fleshy endocarp and two homoplasious forward changes: punctate leaflets and abaxial stomata with a variable number of subsidiary cells, more than two. Our seed observations (Kirkbride et al., 2003) strongly support this relationship (Figs. 1–3). *Cordyla* and *Mildbraediodendron* seeds are large, lack a testa, have straight embryos paralleling the seed length, the radicle tip straight, and the plumule well developed, and are centered relative to the cotyledons.

Pennington et al. (2001) studied the evolution of the basal faboid legumes to clarify the broad-scale relationships within subfamily Faboideae. They carried out phylogenetic analyses using *trnL* intron sequences for 122 taxa, representing 14 of 15 Swartzieae sensu Polhill (1994a, 1994b), 26 of 41 Sophoreae, the 20 Dipterygeae and Dalbergieae, and various placeholders for derived groups; 4 Caesalpinioideae genera were used as outgroups. Using both the *trnL* intron and spacer, Ireland et al. (2000) conducted a phylogenetic analysis focusing on tribe Swartzieae. They sequenced 14 of 15 Swartzieae genera, the genus *Bobgunnia* J. H. Kirkbride & Wiersema, 19 Sophoreae genera, and 20 Dipterygeae and Dalbergieae, using 3 Caesalpinioideae genera as outgroups. Neither study included the Swartzieae genus *Candolleodendron* R. S. Cowan. Both studies used sequences from *Cordyla madagascariensis*, which is here treated as *Dupuya madagascariensis* (R. Viguier) J. H. Kirkbride, and no African *Cordyla* s. str. was included in either study. Their results were similar, differing mainly in scope. Both Swartzieae and Sophoreae are polyphyletic groups whose genera belong in various other tribes. The sister group to the remainder of the faboid legumes is the swartzoid clade (Pennington et al., 2001), consisting of *Bobgunnia*, *Swartzia* Schreber, *Bocoa* Aublet, *Cyathostegia*, and *Ateleia*, which might be recognized as either a redefined tribe Swartzieae or a fourth legume subfamily. Also in both studies, the aldinoid clade (Pennington et al., 2001) consisted of the genera *Myrospermum* Jacquin, *Dussia* Krug & Urban ex Taubert, *Amburana* Schwacke & Taubert, *Mildbraediodendron*, *Dupuya*, and *Aldina* Endlich-

er. Neither of these two clades had been previously recognized in any other study.

The swartzoid and aldinoid clades (except *Aldina*) share absence of the 50-kilobase inversion in the chloroplast genome (Doyle et al., 1996; Ireland et al., 2000), which is also absent from subfamilies Mimosoideae and Caesalpinioideae and present in most of subfamily Faboideae. Because *Aldina* has the CP inversion and the remainder of the aldinoid genera do not, its relationships should be re-examined (Ireland et al., 2000), and more species belonging to the aldinoid clade should be screened for the CP inversion confirming its presence in other genera of this clade, clarifying the circumscription of the clade, and validating the membership of *Dupuya* in it.

Aside from the presence of staminodes and the differences in seed characteristics, *Cordyla* and *Dupuya* are so similar morphologically that they probably are sister genera (sensu Wiley, 1981), and therefore *Cordyla* s. str. also is probably a member of the aldinoid clade. The morphological differences separating genera of the aldinoid clade are presented in the following key.

#### KEY TO GENERA OF THE ALDINOID CLADE

1. Flowers with 1 or (3 to)4 to 7 petals; fruits dehiscent or indehiscent (*Myrospermum*); Neotropics . . . . . 2
- 1'. Flowers without petals; fruits indehiscent; tropical Africa and Madagascar . . . . . 5
- 2(1). Flowers with (3 to)4 to 7 petals; cotyledons with surface grooved, ridged, or rugose, unlobed; embryonic axis oblique or perpendicular to seed length . . . . . 3
- 2'. Flowers with 1 petal (the standard); cotyledons with surface smooth, lobed; embryonic axis parallel to seed length; southeastern Peru to northeastern Brazil and south to northern Argentina . . . . . *Amburana*
- 3(2). Leaflets pellucid-glandular; fruit winged, indehiscent; epicarp veined; seed 10–17 × 4–7.2 × 4.5–5.5 mm; Mexico, Central America, and northern South America . . . . . *Myrospermum*
- 3'. Leaflets not glandular; fruit not winged, dehiscent; epicarp not veined; seed 20–60 × 10–50 × 10–40 mm . . . . . 4
- 4(3). Corolla papilionaceous; fruit elliptic or fusiform, stipitate, with valves enrolling; seed 20–45 × 10–20 × 10–20 mm, not overgrown; testa present; radicle bulbous, straight at tip; Antilles, Mexico, Central America, northwestern South America, and the western Amazon basin . . . . . *Dussia*
- 4'. Corolla not papilionaceous, with petals ± equal; fruit obovate, not stipitate, with valves revolute; seed 35–60 × 30–50 × 22–40 mm, overgrown (1 seed completely filling the fruit cavity); testa absent; radicle triangular, curved at tip; Venezuela and the upper Amazon basin . . . . . *Aldina*

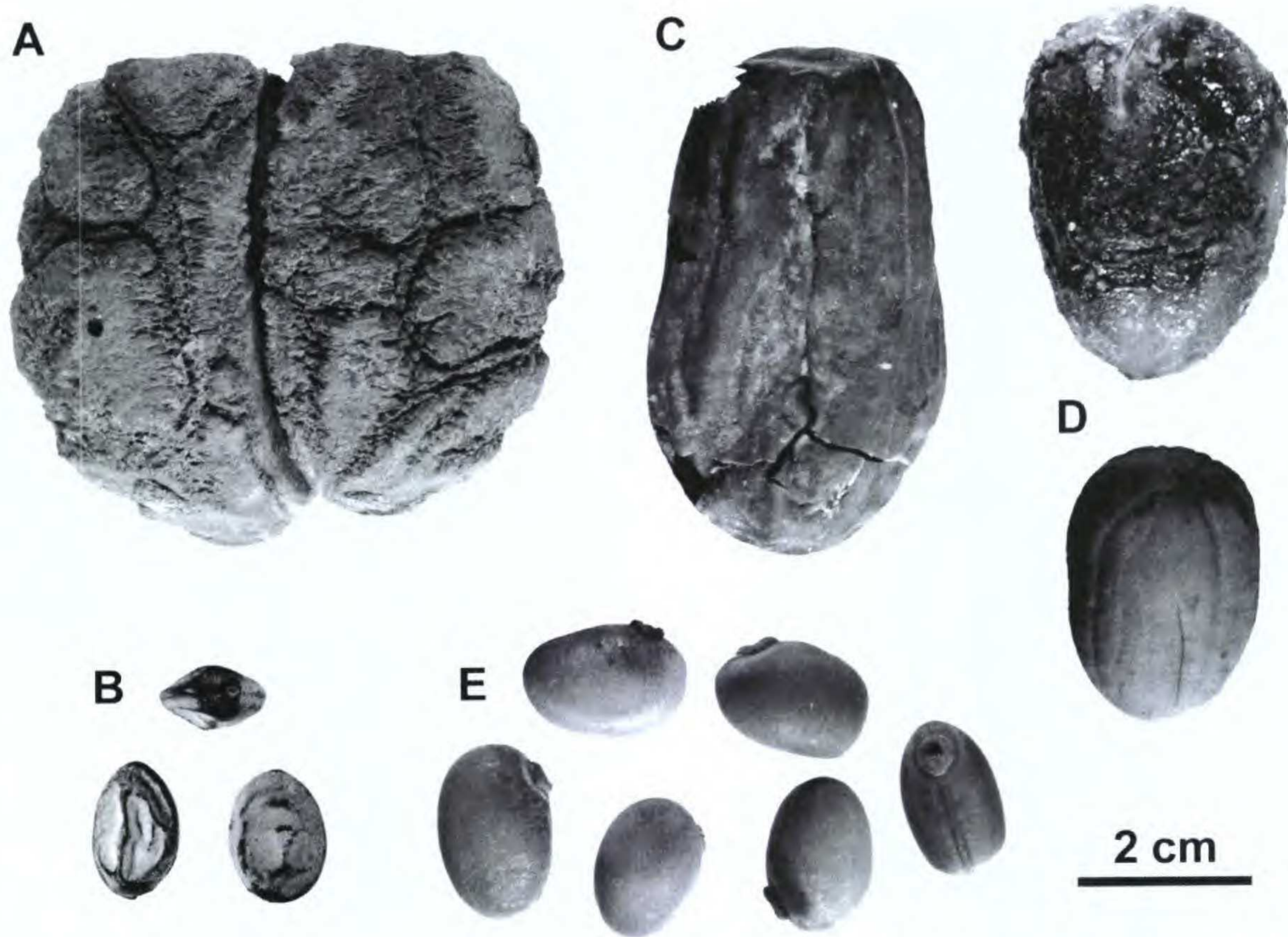


Figure 1. Seeds of *Aldina*, *Amburana*, *Mildbraediendron*, *Cordyla*, and *Dupuya*. —A. Seed of *Aldina latifolia* Bentham (Ducke 24049, BARC). —B. Seeds of *Amburana cearensis* (Allemão) A. C. Smith (PI 109210, BARC). —C. Seed with endocarp of *M. excelsum* Harms (BARC). —D. Seeds with and without endocarp of *C. africana* Loureiro (List #95, Shipment #41, BARC). —E. Seeds with testa of *D. madagascariensis* R. Viguier subsp. *madagascariensis* (Du Puy, Comtet & Labat 2463, P).

- 5(1). Flower buds subglobose, calyx splitting into (2 to)3 unequal lobes down as far as the disc; stamens 12 to 18, basally united into a single whorl at the edge of the disc; tropical Africa . . . . . *Mildbraediendron*
- 5'. Flower buds turbinate, calyx splitting into 2 to 4 unequal to subequal lobes down as far as the apex of the hypanthium; stamens numerous (20 to 130), basally united into approximately 3 or 4 whorls at apex of hypanthium . . . . . 6
- 6(5). Staminodes in a single whorl inside stamens,  $\frac{1}{6}$  to  $\frac{1}{4}$  as long as stamens; testa present, endosperm present, cotyledons folded, partially concealing radicle, one inner cotyledon face with a central ridge and the other with a central groove, embryonic axis oblique to the seed and cotyledon lengths, radicle bulbous; Madagascar . . . . . *Dupuya*
- 6'. Staminodes absent; testa absent, endosperm absent, cotyledons not folded, fully concealing the radicle, inner cotyledon faces flat, embryonic axis parallel to the seed and cotyledon lengths, radicle triangular; tropical Africa . . . . . *Cordyla*

**Dupuya** J. H. Kirkbride, gen. nov. TYPE: *Dupuya madagascariensis* (R. Viguier) J. H. Kirkbride. Figures 1E, 2E, and 3E.

A *Cordyla* et *Mildbraediendro* staminibus multis, staminodiorum verticillo intra stamina, staminodiis staminibus circa quater brevioribus, seminibus brevioribus, arillo, testa, endospermioque praesentibus, cotyledonibus

ambabus plicatis, cotyledonis unius superficie interiore crista et cotyledonis alterius superficie interiore sulco, embryonis axe obliquo ad seminis et cotyledonum axem, radice bulbosa et aliquantum occulta cotyledonibus differt.

Trees, 5–35 m tall, deciduous, the branches with large, corky, cream-colored lenticels, bilobed with the lobes elliptic, parallel to the axis of the branch, with a sulcus between them; stipules small, caducous. Leaves alternate, imparipinnate, with alternate or subopposite leaflets, without stipels, the rachis with 2 narrow adaxial ridges, the closest one of the pair interrupted at each leaflet insertion and the other entire, sometimes extended into stipel-like points, the leaflets emarginate, with glandular streaks oblique to the midrib, sometimes just glandular dots, smaller at the base of the leaf and becoming gradually larger toward the apex of the leaf, “light green above and beneath (drying much darker above)” (Du Puy & Labat, 2002: 294). Inflorescences terminal or rarely axillary, racemose, sometimes flowers solitary in the upper leaf axils, with a caducous bract subtending each pedicel and a pair of bracteoles (sometimes caducous) on the pedicel at ca. the middle or above it. Flowers with a conspicuous hypanthium, the calyx entire, with a tuft of hairs at the apex, splitting into 2 to 4 unequal to subequal lobes, apetalous, the stamens nu-

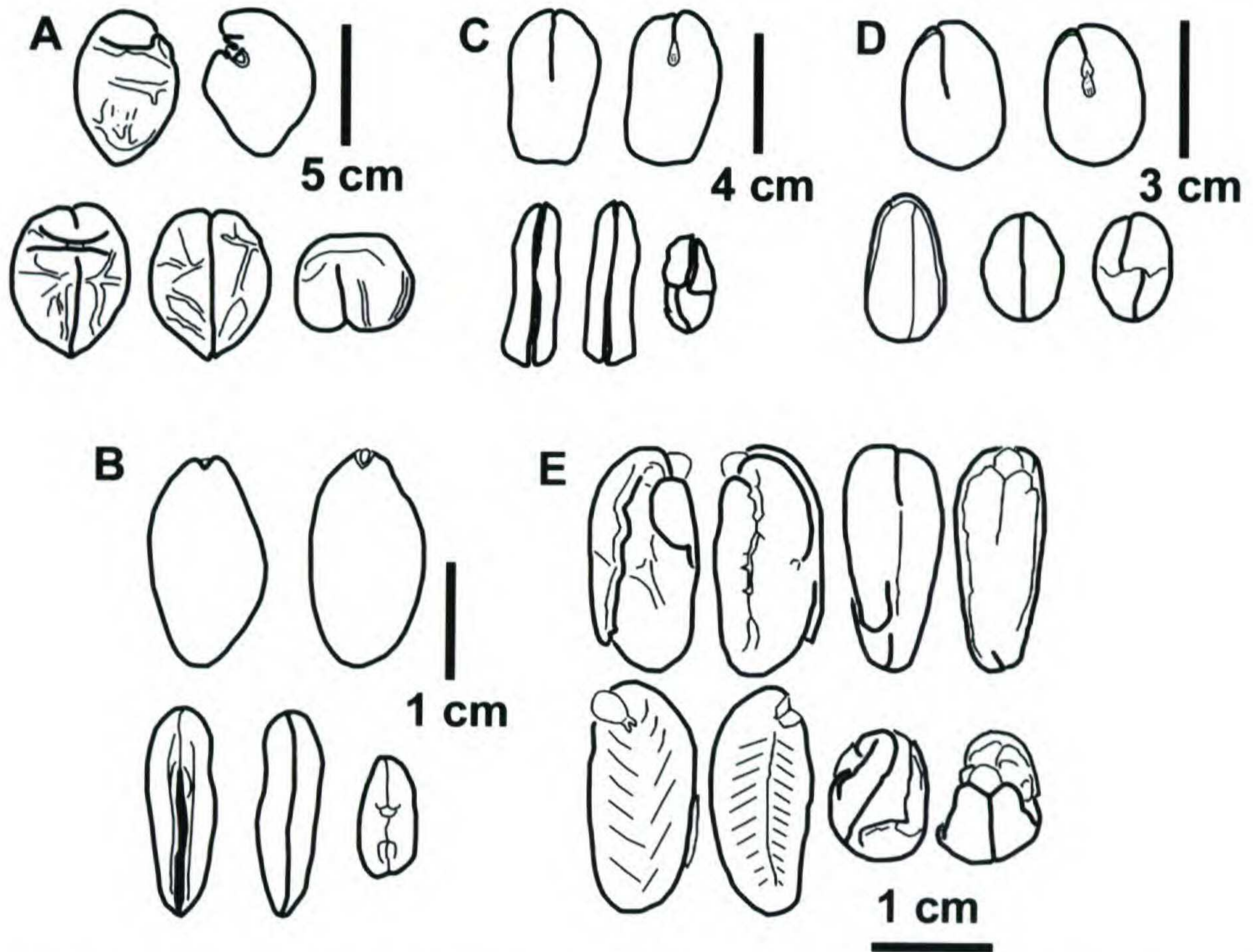


Figure 2. Embryos and cotyledons of *Aldina*, *Amburana*, *Mildbraedi dendron*, *Cordyla*, and *Dupuya*. —A. *Aldina latifolia* (Cid Ferreira et al. 7118, BARC). —B. *Amburana cearensis* (Glaziou 20882, BARC). —C. *M. excelsum* (BARC). —D. *C. africana* (List #95, Shipment #41, BARC). —E. *D. madagascariensis* subsp. *madagascariensis* (R. Capuron s.n., BARC).

merous, approximately arranged in three concentric whorls at the hypanthium apex, with a fourth, inner whorl of staminodes, the filaments basally connate, the anthers elliptic, dorsifixed, longitudinally dehiscent, the staminodes filament-like,  $\frac{1}{6}$  to  $\frac{1}{4}$  as long as the stamens, basally adnate to the stamens, the ovary stipitate, multiovulate, glabrous, exserted above the anthers. Fruits unilocular, straight, elliptic to oblong, terete, with or without a straight beak (5–8 mm long), the same color and texture as fruit, with the apex and base tapered or rounded and aligned with longitudinal axis of fruit; drupaceous when fresh (Du Puy & Labat, 2002) or ligneous when dry, with the margin not constricted or slightly constricted along both margins (when 2 or more seeds in fruit), stipitate, indehiscent; epicarp dull or glossy, light to dark brown or reddish to purplish brown, glabrous, longitudinally ribbed with 20 to 40 ribs; mesocarp thick, 2-layered, ligneous; endocarp dull, white when fresh (Du Puy & Labat, 2002) or pale brown when dry, spongy when dry and disintegrating at the touch, with seeds 1 to 3(4) with their length parallel with fruit length; seeds not overgrown (sensu Corner, 1951), elliptic to oblong or slightly ovate, compressed, with surface smooth, with a dry rim-aril, entire, brown; testa

completely adhering to endocarp, dull, with frequent streaks, reddish to dark brown or red (Du Puy & Labat, 2002), with brown overlay, faintly grooved or striate, coriaceous; raphe from hilum through lens to base of seed and terminating, lighter than testa, reddish brown, recessed; hilum visible, with the lips of the faboid split the same color as the rest of the hilum, elliptic, recessed, within a halo lighter in color than testa; lens not discernible; endosperm thick, covering at least  $\frac{1}{2}$  but not the entire embryo, adnate to testa; cotyledons the same thickness and  $\pm$  of equal length, with 1 to 6 longitudinal grooves on outer faces, with 1 cotyledon partially folded with flaps unequal and not touching and outer face flat, the other fully folded with flaps equal and touching and outer face concave, partially concealing radicle, notched at radicle with lobes touching (auriculate) forming a basal groin, white, inner face of fully folded cotyledon with central ridge and central groove on partially folded one; embryonic axis straight, oblique to seed length; radicle bulbous with lobe tip straight; plumule moderately developed.

The genus is named in honor of David J. Du Puy, senior author of *The Leguminosae of Madagascar*

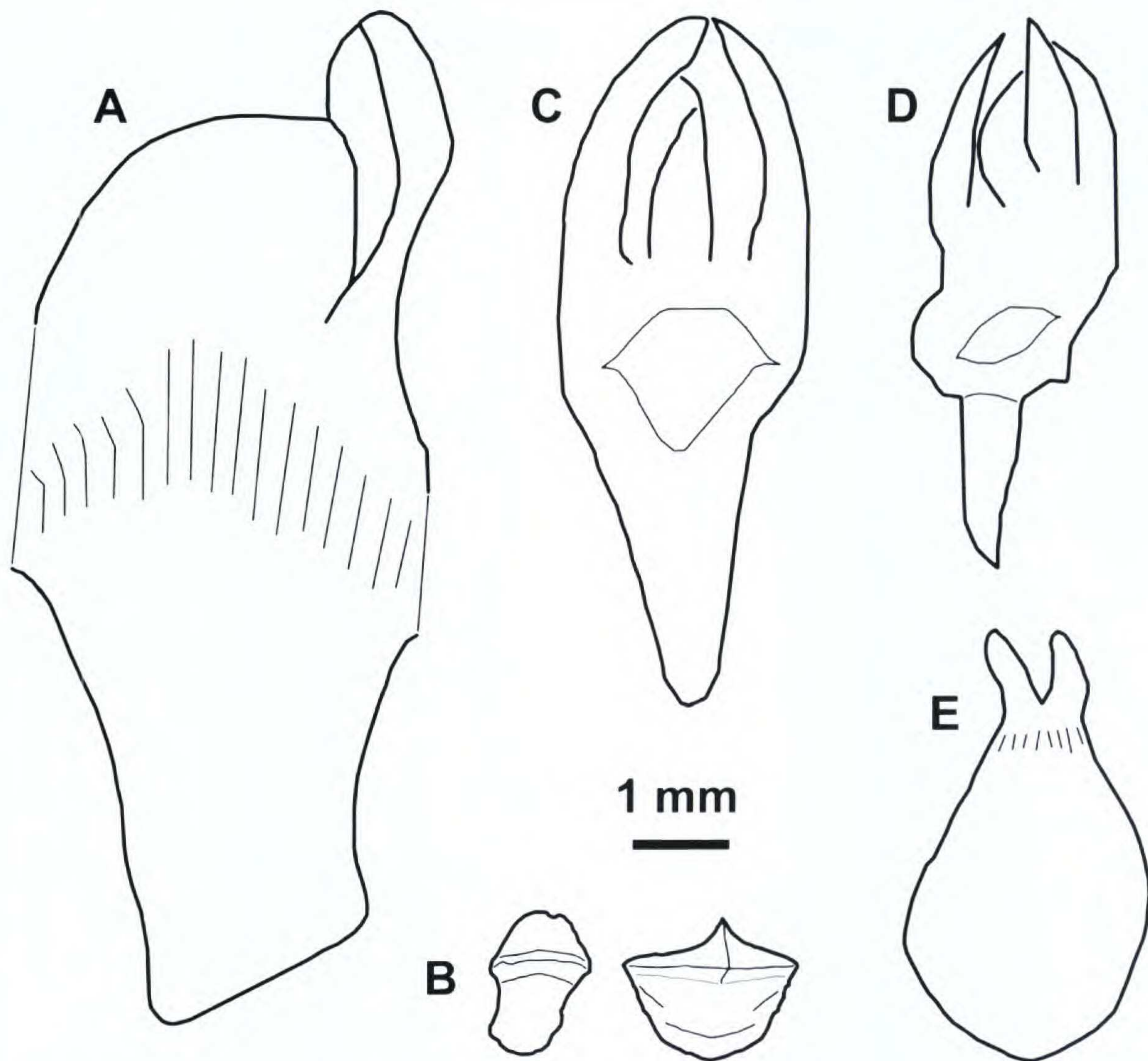


Figure 3. Embryos, with cotyledons removed, of *Aldina*, *Amburana*, *Mildbraedi dendron*, *Cordyla*, and *Dupuya*. —A. *Aldina latifolia* (Cid Ferreira et al. 7118, BARC). —B. *Amburana cearensis* (Glaziou 20882, BARC). —C. *M. excelsum* (BARC). —D. *C. africana* (List #95, Shipment #41, BARC). —E. *D. madagascariensis* subsp. *madagascariensis* (R. Capuron s.n., BARC).

(Du Puy et al., 2002). Du Puy and Labat's (2002) treatment of tribe Swartzieae and the genus *Cordyla* brought this new genus to my attention and supplied essential data enabling its publication.

KEY TO *DUPUYA* SPECIES IN MADAGASCAR

- 1. Stipules straight, obovate to narrowly so; leaves with 6 to 13 leaflets, the petiolules 1–2.5 mm long, the leaflets acute to obtuse at the base, 1–4.5 cm wide; inflorescence bracts elliptic, 2.5–3 × 1–2.7 mm; flower bracteoles elliptic to narrowly so, 3.5–6 × 1.5–2.5 mm; calyx 7–8 mm long; staminodes 3–3.5 mm long; ovary stipe 15–22 mm long; seeds 25 × 14–15 13–15 mm . . . . . *D. haraka*
- 1'. Stipules curved, falcate; leaves with 15 to 44 leaflets, the petiolules 0.5–1 mm long, the leaflets oblique at the base, (0.3–)0.5–1 cm wide; inflorescence bracts narrowly obovate, 1.5–2.5 × 0.5–0.7 mm; flower bracteoles narrowly obovate, 1–2 × 0.4–0.6 mm; calyx 4.5–5 mm long; staminodes 1.5–2.5 mm long; ovary stipe 9–13 mm long; seeds 15–21 × 12–13 × 9–11 mm . . . . . *D. madagascariensis*

**1. *Dupuya haraka*** (Capuron) J. H. Kirkbride, comb. nov. Basionym: *Cordyla haraka* Capuron, *Adansonia*, sér. 2, 8: 220. 1968. TYPE: E Madagascar. Massif de Farankaraina, à l'Est d'Andranofotsy (Maroantsetra), 24 Nov. 1953, *Service Forestier* (R. Capuron) 8658 (holotype, P not seen; isotypes, B not seen, BR not seen, G not seen, K not seen, L not seen, MO, P, WAG not seen).

A large tree 10–35 m tall, DBH 25–100 cm, the “trunk tall, often unbranched except near the crown, flaring basally into rounded buttresses, the bark deep chestnut-brown, flaking off in large irregular pieces, some areas with large corky cream lenticels” (Du Puy & Labat, 2002: 295), youngest branches strigillose with older branches gradually becoming glabrate to glabrous. Stipules straight, obovate to narrowly so, acute at the apex, 1.2–4.5 × 0.4–1.8 mm, strigillose to glabrate. Leaves 8–19 cm long, with 6 to 13 leaflets, the rachis 6–13 cm

long, strigillose to glabrate, the petiolules 1–2.5 mm long, strigillose to glabrate, with the blade obovate to rarely broadly so or elliptic to rarely broadly so, acute to obtuse at the base, emarginate to sometimes obtuse to acute at the apex,  $1.3\text{--}8.5 \times 1\text{--}4.5$  cm, strigillose to glabrate with hairs concentrated over the midrib and veins, “becoming deep green and glossy above, pale green beneath” (Du Puy & Labat, 2002: 295), coriaceous to chartaceous. Racemes terminal or rarely axillary, (1- to)9- to 22-flowered, (3–)6–14 cm long, the bracts elliptic, obtuse to subacute at the apex,  $2.5\text{--}3 \times 1\text{--}2.7$  mm, strigillose, the pedicels 4.5–10 mm long, strigillose to glabrate, with the bracteoles elliptic to narrowly so, acute to obtuse at the apex,  $3.5\text{--}6 \times 1.5\text{--}2.5$  mm, glabrate to sparsely strigillose, the hypanthium expanding upward, 2.5–4 mm long, 2–3.5 mm diam. at the base and 3.2–4.5 mm diam. at the apex, strigillose to glabrate outside and glabrous inside, the calyx 7–8 mm long, glabrous to glabrate outside and sericeous inside, the filaments unequal, 11–19 mm long, glabrous, the anthers 0.7–1 mm long, glabrous, the staminodes 3–3.5 mm long, the stipe 15–22 mm long, 0.7–0.8 mm diam., glabrous, the ovary  $4.5\text{--}6 \times 1.5\text{--}2$  mm, glabrous, the style 3–5 mm long, glabrous. Fruits ellipsoid to clavate, with a beak 2–4 mm long,  $4\text{--}7 \times 2\text{--}3.5$  cm, glabrous, with the stipe 2–3 cm long. Seeds  $25 \times 14\text{--}15 \times 13\text{--}15$  mm.

*Illustrations.* Capuron (1968: fig. 5, p. 221); Du Puy & Labat (2002: fig. 55, G–J, p. 296, pl. 18, A).

*Habitat and distribution.* From Toamasina to Vohemar, southeast of Antsiranana, and also on the island of Nosy Bé and the Ankarana Massif in Madagascar. Found up to 700 m, in tall evergreen rainforest and also in deciduous forest in the north (Du Puy & Labat, 2002).

*Common names.* Haraka (*Service Forestier* (R. Capuron) 8658, P); Harakafotsy (*Service Forestier* 15711, P); Vahonda (Du Puy & Labat, 2002).

Most individuals of this species are found in the eastern, evergreen, low-altitude forests, without a distinct dry season and very high annual rainfall, from Toamasina to Vohemar. At the northern end of its range, the species stretches across Madagascar at approximately 13°S latitude into the evergreen, Sambirano, low-altitude forests, with a distinct dry season of 4 to 6 months and high annual rainfall, from the vicinity of Vohemar to the island of Nosy Bé. The morphology of specimens from the eastern forests differs slightly from those collected in the Sambirano forests. The eastern-forest specimens have, in general, slightly larger structures, for ex-

ample, stems bigger in diameter, larger leaflets and flowers, longer inflorescences, as well as more coriaceous leaflets than the Sambirano-forest specimens. The Sambirano-forest specimens are intermediate in some characteristics between the eastern-forest specimens and *D. madagascariensis*.

*Specimens examined.* MADAGASCAR. E Madagascar, Masoala Peninsula, western side, NE of Antalavia, 4 hours on foot along Antalavia River (ca. 4–5 km ?), 15°46'S, 50°2'E, 285 m, 16 Nov. 1989, D. J. Du Puy, B. P. Du Puy, G. Rafamantanantsoa & G. Schatz M375 (P); Toamasina, Diego Suarez region, SE of town and SE of Ambilobe, near Daraina on road to Vohemar (Iharana), D. Meyer's lemur study site, 14°70'S, 49°46'E, 200 m, G. McPherson 14735 (K, MO); District Fénérive, dans le forêt de Bemahogo, 2 km 500 à l'est du village de Andapibe et d'Ambodranpana, 30 Mar. 1952, *Rakotoniaina* 8 (MO); Toamasina, Masoala Peninsula, just E of Ambanizana in hills above village, 15°38'S, 49°58'E, 10–200 m, 24 Nov. 1989, G. E. Schatz & P. P. Lowry II 2836 (MO); Farankaraina, à l'est d'Andranofotsy (Maroantsetra), 24 Nov. 1953, *Service Forestier* (R. Capuron) 8658 (P); forêt orientale, forêt d'Antandrokaolo, entre Morafeno, sur la Rantabe et Amboditavolo, bassin de la Fananehana, 400 m, Feb. 1954, *Service Forestier* (R. Capuron) 9029 (K, P); Ouest (Nord), Plateau de l'Ankarana entre les P.K.84-85 (entre Anivorano-Nord et Ambondromifehy), 14 Nov. 1958, *Service Forestier* (R. Capuron) 20004 (MO, P); Ouest (Nord), vestige de forêt entre Belinta et Ambetratra, à quelques kilomètres au NW de Vohémer, 14 Oct. 1966, *Service Forestier* (R. Capuron) 24853 (K, MO, P); Ouest (Nord), vestige de forêt entre Belinta et Ambetratra, au NW de Vohémer, au Sud de Maintialaka, 10–18 Dec. 1966, *Service Forestier* (R. Capuron) 27337 (MO, P); forêt d'Amboangisay, Canton d'Ampahano-Antalaha, 20 June 1952, *Service Forestier* 133R.140 (MO); Tampolo, Fénérive, 13 Nov. 1954, *Service Forestier* 12479 (MO, P), 2 Mar. 1955, *Service Forestier* 13100 (BARC, P); Farankaraina, Maroahitra, 5 Mar. 1956, *Service Forestier* 15711 (BARC, K, P).

**Dupuya madagascariensis** (R. Viguier) J. H. Kirkbride, comb. nov. Basionym: *Cordyla madagascariensis* R. Viguier, *Notul. Syst.* (Paris) 13: 355. 1949. TYPE: W Madagascar. Bassin du Fiherenana, 400 m, Oct. 1926, H. Perrier de la Bâthie 16617 (lectotype, designated by Du Puy & Labat (2002: 295), P not seen; isotypes, K not seen, MO not seen, P). Figures 1E, 2E, and 3E.

A tree 5–25 m tall, DBH 15–70 cm, “the bark with shallow fissures forming a net pattern, eventually flaking off in large pieces, pale grey-brown” (Du Puy & Labat, 2002: 295), youngest branches strigillose with older branches gradually becoming glabrate to glabrous. Stipules curved, falcate, narrowly acute at the apex,  $3\text{--}4 \times 0.2\text{--}0.7$  mm, strigillose to densely so. Leaves (7–)14–22 cm long, with 15 to 44 leaflets, the rachis (6–)12–18.5 cm long, strigillose to glabrous, the petiolules 0.5–1

mm long, strigillose to glabrate, with the blade narrowly obovate to narrowly elliptic, oblique at the base, emarginated at the apex, with entire to crenate margins, (0.6–)1.4–3.6 × (0.3–)0.5–1 cm, glabrate to glabrous with hairs concentrated over the midrib and veins, “pale green (often drying darker above)” (Du Puy & Labat, 2002: 295), chartaceous. Racemes terminal, rarely axillary, or sometimes a solitary flower in the upper leaf axils, 1- or (10- to)12- to 38-flowered, 6–18 cm long, the bracts, pedicels, and bracteoles strigillose to glabrate, the bracts narrowly obovate, narrowly acute at the apex, 1.5–2.5 × 0.5–0.7 mm, the pedicels 3–6 mm long, with the bracteoles narrowly obovate, narrowly acute at the apex, 1–2 × 0.4–0.6 mm, the hypanthium expanding upward, 1.5–2 mm long, 1.1–2 mm diam. at the base and 1.5–2.5 mm diam. at the apex, glabrous to glabrate outside and glabrous inside, the calyx 4.5–5 mm long, glabrous outside and sericeous to sparsely so inside, the stamens glabrous; the filaments unequal, 9–15.5 mm long, the anthers 0.5–0.8 mm long, the staminodes 1.5–2.5 mm long, the gynoecium glabrous, the stipe 9–13 mm long, 0.5–0.7 mm diam., the ovary 3–4.5 × 1.5–2 mm, the style 1.5–4.5 mm long. Fruits ellipsoid to cylindrical to moniliform, with a beak 2–8 mm long, 3–6.5 × 2–3 cm, glabrous, with the stipe 2–3.5 cm long; seeds 15–21 × 12–13 × 9–11 mm.

*Illustration.* Du Puy & Labat (2002: pl. 18, B).

*Common names.* Anakaraka (*M. F. C. Louvel 160*, P); Hazomena (*Service Forestier (R. Capuron) 3031*, P); Karabo (*Service Forestier 2838*, P); Landrazo (Du Puy & Labat, 2002); Lazaza (Du Puy & Labat, 2002); Madiroala (*Du Puy et al. M755*, P); Madivoala (Du Puy & Labat, 2002); Maimbohazo (Du Puy & Labat, 2002); Sikilihazo (Du Puy & Labat, 2002); Vaivay (Du Puy & Labat, 2002).

KEY TO SUBSPECIES OF *DUPUYA MADAGASCARIENSIS* IN MADAGASCAR

1. Stipules 3.5–4 × 0.2–0.3 mm; leaflets 17 to 30(to 40); staminodes ca. 1.5 mm long; fruit beak 5–8 mm long . . . . . *D. madagascariensis* subsp. *madagascariensis*  
1'. Stipules 3–3.5 × 0.5–0.7 mm; leaflets (19 to)38 to 44; staminodes 2–2.5 mm long; fruit beak 2–5 mm long . . . . . *D. madagascariensis* subsp. *tamarindoides*

There are two subspecies recognized for *Dupuya madagascariensis* in Madagascar, one of which, the non-autonym, needs a new combination.

***Dupuya madagascariensis* subsp. *madagascariensis*.** *Cordyla madagascariensis* var. *madagascariensis*, *Adansonia*, sér. 2, 8: 220. 1968. *Cordyla madagascariensis* subsp. *madagascariensis*,

*in* Du Puy et al., *Leg. Madagascar* 297. 2002. TYPE: W Madagascar. Basin du Fihrenana, 400 m, Oct. 1926, *H. Perrier de la Bâthie 16617* (lectotype, designated by Du Puy & Labat (2002: 295), P not seen; isotypes, K not seen, MO not seen, P). Figures 1E, 2E, and 3E.

*Illustration.* Du Puy & Labat (2002: fig. 55, A–F, p. 296).

*Specimens examined.* MADAGASCAR. 40 km d’Ankazoabo, route Sakaraha, Feb. 1970, *J. Bosser 19956* (P); W Madagascar, Province of Toliara (Tulear), NE of Morondava, ca. 4 km NE of Andranomena, route to Marofandila, 20°9’S, 44°27’E, 30 m, 20 Oct. 1989, *D. J. Du Puy, B. P. Du Puy & J. Andriantiana M361* (K, P); W Madagascar, Toliara Province, Forest of Kirindy, ca. 60 km NNE of Morondava (Swiss Forestry Concession, “Piste Conoco”), 20°5’S, 44°37’E, ca. 30 m, 18 July 1989, *D. J. Du Puy, B. P. Du Puy & D. Baum M297* (K, P); Tulear, Tulear, Manombo, Forêt de Mikea, env. 2 km au N de Beroroha, 22°52’54”S, 43°33’25”E, 60 m, 6 Dec. 1993, *J.-N. Labat, D. J. Du Puy & S. Comtet 2463* (BARC, MO, P); Tsinembo, 21 Oct. 1932, *J. Leandri 444* (P); Trangahy, 31 Oct. 1932, *J. Leandri 481* (MO, P), *J. Leandri s.n.* (P); forêt à feuilles caduques sur calcaires de l’Antsingy, vers Ambodiriana (E d’Antsalova), 100–150 m, 21–27 Jan. 1960, *J. Leandri & P. Saboureau 2751* (MO); forêt à feuilles caduques sur calcaires de l’Antsingy, vers Andobo (E d’Antsalova), 100–150 m, 7 Feb., *J. Leandri & P. Saboureau 3037* (MO, P); forêts de l’Ouest, Anakarake, Morondava, Feb. 1923, *M. Louvel 160* (P; syntype of *Cordyla madagascariensis*); Toliara, 55 km NE of Morondava via route 8 at the forestry concession of the Centre de Formation Professionnelle Forestière (CFPF), Kirindy Forest, 5 km E of route 8 along principal concession road (Piste CONOCO), along S boundary of forestry block, 20°4’S, 44°40’E, 35 m, 21 Mar. 1992, *R. D. Noyes, D. K. Harder, E. A. Rakotobe, T. G. Razafindrabeaza & J. P. Abraham 1053* (MO); Toliara, N of Toliara, in Forêt de Mikea, ca. 18 road-km W of Vorehe, 22°15’S, 43°25’E, 50 m, *G. McPherson, S. Razafimandimbison, M. Olsen & B. Alongi 17354* (MO); Bois de Bona (Ankazoabo) sud, Feb. 1970, *P. Morat 3574* (MO); Ankaladiny, sur la Bebibokn, July 1904, *H. Perrier de la Bâthie 1414* (P; syntype of *Cordyla madagascariensis*); sur le Manambato, Oct. 1913, *H. Perrier de la Bâthie 4240* (P; syntype of *Cordyla madagascariensis*); environs de Majunga, à Ankatsepe, Aug. 1914, *H. Perrier de la Bâthie 4749* (P; syntype of *Cordyla madagascariensis*); Toliara, Zombitsy Forest, along Route Nationale 7, 10 km from Sakaraha, 22°54’S, 44°38’E, 650 m, 27 Feb. 1990, *P. B. Phillipson & J. R. Milijaona 3639* (MO); Toliara, Préfecture Morondava, approximately 60 km (by road) NE of Morondava, in the Kirindy Swiss forestry concession, 20°5’S, 44°38’E, 45 m, 25–31 Oct. 1990, *G. E. Schatz 2982* (MO); Ampandra, Tulear, 22°56’S, 44°32’E, 6 Feb. 1951, *Service Forestier 2838* (P); Belo/Tsiribihina, forêt d’Andranofotsy, 8 Jan. 1955, *Service Forestier 13154* (MO); T. Ankatoky, Beroroha, 16 May 1955, *Service Forestier 13295* (MO).

**Dupuya madagascariensis** subsp. **tamarindoides** (Capuron) J. H. Kirkbride, comb. nov. Basionym: *Cordyla madagascariensis* var. *tamarindoides* Capuron, *Adansonia*, sér. 2, 8: 220. 1968. *Cordyla madagascariensis* subsp. *tamarindoides* (Capuron) D. J. Du Puy & Labat, in Du Puy et al., *Leg. Madagascar* 297. 2002. TYPE: N Madagascar. Plateau calcaire de l'Ankarana, environs d'Ambondromifehy, *Service Forestier (R. Capuron) 3031* (holotype, P not seen; isotypes, K not seen, MO not seen, P).

*Specimens examined.* MADAGASCAR. District d'Ambilobe, montagne d'Andavakafanihy, calcaires de l'Ankarana, km 105 de la route d'Ambilobe, 200 m, 3 Feb. 1960, G. Cours & H. Humbert 5620 (P); N Madagascar, Antsiranana Province, SE of Antsiranana (Diego Suarez), NW of Irodo village, Analafandrika forest, 12°38'2"S, 49°31'40"E, 60 m, 24 Mar. 1994, D. J. Du Puy, J. Andriantiana & O. Andrianantoanina M755 (K, P); N Madagascar, Antsiranana Province, "Windsor Castle" peak near Ilomotro, NW of Antsiranana (Diego Suarez), 12°13'N, 49°10'E, 200 m, 10 June 1989, D. J. Du Puy, B. P. Du Puy & G. Rafamantanantsoa M267 (K, P); Antsiranana, Vovo Village Distr., ca. 6 km from Diego Suarez on Diego Suarez-Vovo Village road, and ca. 1.5 km S of beach on Indian Ocean, 12°19'5"S, 49°23'7"E, 85 m, 23 Apr. 1993, D. K. Harder, M. C. Merello, S. G. Razafiman-dimison & T. G. Razafinfrabaeza 1693 (MO); plateaux calcaires de l'Ankarana du nord entre Ambilobe et Anivorano, 12°57'S, 49°8'E, 200–350 m, 4–9 Mar. 1951, H. Humbert & R. Capuron 25485 (P); Province de Diego-Suarez, collines et plateaux calcaires de l'Ankarana du nord, vers grotte du Fanihy, 30–350 m, 24 Jan.–29 Feb. 1960, H. Humbert & G. Cours 32728 (P); Antsiranana, Ambilobe, Matsaborimanga, Réserve Spéciale gd'Ankarana, Tsingy au dessus du lac Vert, 12°55'26"S, 49°5'10"E, 300 m, 20 Nov. 1996, J.-N. Labat, E. Randrianjohany & O. Andrianantoanina 2790 (P); Antsiranana, Ambilobe, Matsaborimanga, Réserve Spéciale d'Ankarana, piste du lac Vert, début de la zone calcaire, avant Amposatelo, 12°55'7"S, 49°5'46"E, 180 m, 21 Nov. 1996, J.-N. Labat, E. Randrianjohany & O. Andrianantoanina 2803 (P); Antsiranana, Réserve Spéciale d'Ankarana, piste vers le lac Vert, plaque du Tsingy, 12°54'43"S, 49°6'39"E, 180 m, 18 Feb. 1994, P. J. Rakotomalaza 142 (MO); NW Madagascar, Antsiranana province, Ankarana Reserve, 3.4 km from Ambondromifehy, 12°52'S, 49°14'E, ca. 220 m, B. D. Schire, D. J. Du Puy & G. P. Lewis 2542 (MO, P); Marofandilia, Bevoay-Morondava, 14 Nov. 1952, *Service Forestier* 6062 (P); Andranolava-Tuléar, Forêt de Vohibasiasia, 15 Jan. 1954, *Service Forestier* 8296 (P); Montagne des Français-Diego Suarez, *Service Forestier* 12731 (K, P); District Morondava, Canton de Befasy, Pente moyenne, Anadabo, 8 Oct. 1956, *Service Forestier* 16555 (MO, P).

Du Puy and Labat (2002: 297) gave the distribution of *Dupuya madagascariensis* from southwestern to northern Madagascar in seasonally dry forest with a dry season of 6 to 8 months, found up to ca. 500 m elevation, from the Forest of Sakaraha to Antsiranana. *Dupuya madagascariensis* subsp.

*madagascariensis* has the largest distribution of the two subspecies throughout southern and southwestern Madagascar, and *D. madagascariensis* subsp. *tamarindoides* occurs at the northern tip of Madagascar, mainly to the north of the Ankarana and Analamerana Massifs (Du Puy & Labat, 2002: 297). *Dupuya haraka* and *D. madagascariensis* are allopatric, except for their populations on the Ankarana Massif. According to Du Puy and Moat's (2002: map 4) vegetation zones, the Ankarana Massif has both humid Sambirano forests and seasonally dry forests. The herbarium labels are not sufficient to determine the exact habitat of each species on the Ankarana Massif, but they are sympatric.

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APPENDIX I. *CORDYLA* SPECIMENS EXAMINED.

***Cordyla africana*** Loureiro

**KENYA.** Lamu District, Witu Forest near Mambosasa Game Forest Post, 2°23'S, 40°32'E, 10–20 m, 20 Feb. 1977, R. B. Faden & A. J. Faden 77/567 (BARC, MO, P); Kilifi District, Pangani, crossing of Lwandani Stream on Chonyi–Ribe road, 3°51'S, 39°41'E, 160 m, 16 Feb. 1977, R. B. Faden, A. J. Faden, J. B. Gillett & N. Gachathi 77/447 (MO, US); Lamu District, Witu Forest, N of road, forest at northern point of reserve and up to 1 km S, 16 Nov. 1988, S. A. Robertson & Q. Luke 5488 (K, US); Kwale District, Mrima Hill, 10 Apr. 1978, B. Verdcourt 5274 (K). **MALAWI.** Mangochi District, Monkey Bay/Mangochi road, roadside, J. L. Balaka, A. J. Salubeni & R. B. Kwatha 1282 (MO); Machinga District, Liwonde, roadside, 14 Aug. 1986, A. J. Salubeni, J. L. Balaka & C. A. Musa 4699 (MO); Zomba District, Chigwere Village, Chisi Island, Lake Chilwe, Chisi Hill slopes, 10 Nov. 1986, A. J. Salubeni & R. B. Kwatha 4850 (MO); Zomba District, Zomba Botanic Garden, edge of Mulunguzi river, 21 Oct. 1987, E. J. Tawakali & M. S. Thera 1152 (MO). **MOZAMBIQUE.** Gaza, entre Javanhana e Caniçado, próximo do rio Limpopo, 9 Oct. 1958, L. A. Grandvaux Barbosa 8348 (K); Province du Gorongosa, Village di Sabinha, Rivier du Vunduzi, 23 Sep. 1906, G. Vasse 418 (P). **SOUTH AFRICA.** Zululand, St. Lucia, western shores, Hell's Gate Peninsula along side road, 30.5 m, 12 Mar. 1982, A. Nicholas & D. MacDevette 1276 (MO). **TANZANIA.** Mtwara District, Tangazo Village, 30 km S of Mtwara on road to Maharunga and Ruvuma R. mouth, 6 Nov. 1978, F. C. Magogo & R. R. Innes RRI476 (K); Moshi District, Moshi–Arusha road, 19 Nov. 1951, McCoy-Hill 19 (K); Bezirk Lindi, Lutamba-See, 40 km westlich Lindi, 200–250 m, 7 Sep. 1934, H. J. Schlieben 5267 (P); Eastern Province, Kilosa District, Old Boma, 18 Oct. 1961, S. R. Semsei 3320 (K). **ZAMBIA.** Eastern Province, foothills E of Machinje Hills, 1000 m, 12 Oct. 1958, N. K. B. Robson 66 (K). **ZIMBABWE.** District Mrewa, Uzumbi Tribal Trust Land, Chiore School Road, 5 Oct. 1969, H. D. L. Corby 2138 (K); District Mrungwe, Mana Pools, Sep. 1969, T. A. S. Gordon 44 (K); Sabi valley, above 549 m, 23 Mar. 1905, W. M. Longden 13132 (US); Causeway, 1975, National Botanic Garden s.n. List #50 Shipment #10 (BARC); Weller s.n. List #95 Shipment #41 (BARC).

***Cordyla densiflora*** Milne-Redhead

**TANZANIA.** Mpwapwa, 1067–1219 m, 18 June 1933, B. D. Burt 4755 (K); Iringa Province, Iringa, 914–1219 m, 18 Sep. 1936, H. E. Emson 618 (K); Iringa District, Msembe, 823 m, Apr. 1970, P. J. Greenway 4420 (K); Msembe, near the Rest House, 762 m, 5 Aug. 1969, P. J. Greenway & Kanuri 13690 (K); Morogoro Region, Morogoro District, Ruaha gorge on Morogoro–Iringa road, 36°40'S, 7°30'E, 26 June 1986, J. Lovett & J. Lovett 852 (K); Iringa District, Nyangolo, 16 July 1956, E. Milne-Redhead & P. Taylor 11223 (K); Iringa District, Ruaha National Park, Kimiramatonge Hill, 823 m, 23 Oct. 1970, H. M. Richards & S. Arasululu 26323 (BARC, K).

***Cordyla pinnata*** (A. Richard) Milne-Redhead

**GAMBIA.** Near Georgetown, 10 Jan. 1927, J. M. Dalziel 8029 (K); bords de la Gambia, Mar. 1829, G. S. Perrottet s.n. (P). **GUINEA.** Région de Gaoual, près Koumbia, 14 Jan. 1979, S. Lisowski 51176 (K). **MALI.** Diondiou, 16 June 1899, A. Chevalier 3345 (P); Kakoulou (Kayes), 11

Jan. 1937, *R. Dubois* 248 (P); à 18 km de Ségou en direction de Mopti, 14 May 1989, *D. Gautier-Béguin & L. Gautier-Béguin* 1414 (MO). **NIGERIA.** Province Niger, District Mokwa, 29 Dec. 1964, *D. P. Stanfield* 55965 (K). **SENEGAL.** Thiès-Diourbel, Kaolack, 23 Mar. 1954, *R. P. Berhaut* 4945 (P); Sédhiou (Casamance), Feb. 1900, *A. Chevalier* 3537 (P), *Heudelot* 367 (P); Boundou, Woulli, 1836, *Heudelot s.n.* (P); Belidjibara, 99 km après Kous-saus, Sausaué, 15 Feb. 1983, *P. Lavie* 1720 (P), *G. S. Perrottet* 32 (P), *s.n.* (P); Km 220 entre Diourbel et Gas-sane, 11 Dec. 1930, *J. Trochain* 1114 (P); Tambacounda-Diabougou-Vélingara, 21 June 1931, *J. Trochain* 1258 (P).

***Cordyla richardii*** Milne-Redhead

**SUDAN.** Waw, Bahr Al Ghazal, 28 Feb. 1926, *G. Aylmer* 27/23 (K); Waw, *A. H. Braun s.n.* (K); Imatong Mountains, just S of Ngarama along the road to Molongori, near the northernmost point of the continuous chain, 700 m, 13 Mar. 1982, *I. Friis & K. Vollesen* 1186 (K). **UGANDA.**

West Madi district, at Metuli, 1219 m, Dec. 1931, *N. V. Brasnett* 309 (K); Metu, Madi, ca. 1 mi. SW of Metu rest-house, on S side of Dzele hill, 1158 m, 5 Dec. 1947, *H. C. Dawkins* 302 (K).

***Cordyla somaliensis*** J. B. Gillett subsp. ***littoralis***  
J. B. Gillett

**SOMALIA.** Merca, 29 Jan. 1954, *Bally* 9527 (K).

***Cordyla somaliensis*** J. B. Gillett subsp. ***somaliensis***

**ETHIOPIA.** Oagden: W of Warder, 6°50'N, 44°10'E, 914 m, 16 Oct. 1953, *E. Ellis* 126 (K); 10 mi. SW Warder, 16 Oct. 1954, *C. F. Henning* 371 (K); 4 mi. E of Mersin, 15 July 1958, *C. F. Henning* 1557 (K). **SOMALIA.** 17 km S of Gellinsoor, 520 m, 7 Feb. 1973, *P. R. O. Bally & R. Melville* 16283 (K); ca. 10 km from Bula Burti to Ceel Buur, 4°0'N, 45°30'E, 15 May 1979, *A. A. Elmi & O. J. Hanson* 4019 (K).